THE SYSTEMATIC POSITION OF THE PSAMMINAE
(Heteroptera: Lygaeidae)[1]

JAMES A. SLATER[2] *and* MERRILL H. SWEET[3]

Bergroth (1921) erected the tribe Psammini to include two monotypic genera, *Psammium* Breddin from South Africa and *Sympeplus* Bergroth from India. The tribe was placed by Bergroth in the lygaeid subfamily Geocorinae chiefly because of the large protruding "reniform" eyes possessed by members of this latter subfamily.

We have recently had occasion to examine members of both genera of Psammini and find that they do not belong to the Geocorinae and cannot be placed within any existing subfamily of Lygaeidae on the basis of our present subfamilial concepts. In this paper we review the relationships of these curious insects in an attempt to ascertain their systematic position and conclude that they are lygaeids rather than members of related "lygaeoid" families, and that they should constitute a distinct subfamily.

Both *Psammium* and *Sympeplus* are very small insects, not exceeding 2½ mm. in length. The mesothoracic wings are highly modified into a complete "coleopteroid" shell which lacks a membrane, has the clavus and corium indistinguishably fused, completely covers the abdomen, is strongly convex and meets in a straight line down the middle of the dorsum. The hind wings are lacking. The body is nearly uniformly coarsely punctate, the eyes large and reniform, the antennae short and subclavate, the legs short and rugose but not distinctly fossorial. It seems evident that both genera are adapted for some type of cryptic habitat, although nothing is known of their biologies.

The systematic position of these insects is very difficult to ascertain for not only do they have a number of features which appear to be of phylogenetic significance, but they also present a number of other characters which may be better interpreted as reduction phenomena. Some of these modifications may be associated with the wing modifications for a specialized habitat.

We propose in the following discussion to compare the Psamminae to allied families of Lygaeoidea and then to subfamilies of the family Lygaeidae itself.

a. *Family Position*:

Both *Psammium* and *Sympeplus* possess dorsally located spiracles on all abdominal segments normally bearing these structures which

[1] This work was supported by grants from the National Science Foundation and the University of Connecticut Research Foundation.

[2] Department of Zoology and Entomology, University of Connecticut, Storrs, Connecticut.

[3] Department of Biology, Texas A & M University, College Station, Texas.

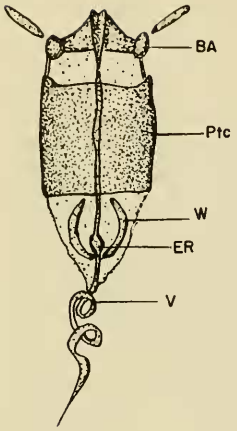

Fig. 1

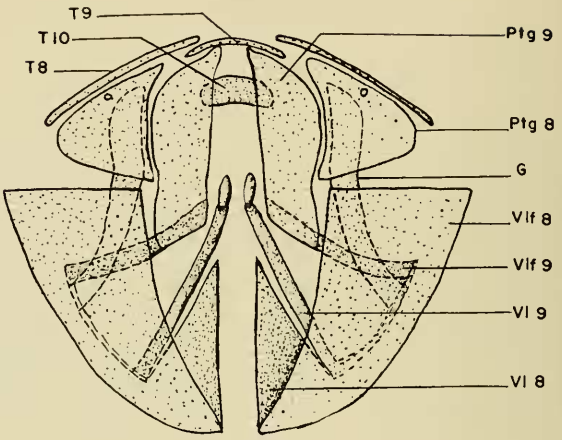

Fig. 2

Fig. 1. Aedeagus of *Psammium*. BA—Basal apparatus; Ptc—Phallotheca; W—Wings; ER—Ejaculatory reservoir; V—Vesica. Fig. 2. Ovipositor of *Psammium* slightly spread; posterior view. T—Tergum; Ptg—Paratergite; Vlf—Valvifer; Vl—Valvulae; G—Gonagulum.

indicates possible relationships to the Berytinidae, where all spiracles are dorsal, or to the Piesmatidae where only spiracle seven is ventral (*McAteella*, *Miespa*), or six and seven are ventral (*Piesma*). However, it is at once apparent that the Psamminae cannot be derived from either of these families (or the reverse) for the psammines have the dorsal scent gland orifices located between terga 4–5 and 5–6, whereas both the Berytinidae and Piesmatidae possess these openings between terga 3–4 and 4–5. This fundamental character is definite evidence that the psammini have been independently derived from the generalized condition of orifices between terga 3–4, 4–5 and 5–6 and thus cannot be considered as belonging to either the Berytinidae or the Piesmatidae.

The Psamminae show no direct relationship to the Berytinidae other than the presence of dorsal spiracles. The relationship to the Piesmatidae, however, is more interesting and more complex. Both taxa show marked reduction in the trichobothrial pattern with no trichobothria on segments four and seven, and a single one located mesally on segment five. The reduction phenomenon has gone even further in the Piesmatidae where segment six also has a single trichobothrium, whereas two are present in the Psamminae. Both taxa also have only two tarsal segments, lack ocelli, and agree in such features of the phallus as the lack of phallothecal lobes, helicoid process, and in having only a small thickening to represent the sperm reservoir. However, the piesmatids have a coiled spermatheca (Drake and Davis 1958)

whereas in the psammines it is a short duct with a terminal bulb; the psammines lack the characteristic propleural cavities and paranota of the piesmatids; the inner laterotergites are absent in piesmatids and present in the psammines (although reduced) and the phallus of the piesmatids lacks long wings and has a long coiled gonoporal process.

We consider, therefore, that the seeming similarities between the Piesmatidae and Psamminae are parallel evolutionary developments rather than indications of phylogenetic relationship. The fact that all of the similarities are reduction phenomena—some of which, such as two-segmented tarsi and trichobothrial reduction are already known to be attained quite independently several times in the Heteroptera—strengthens our contention that these two taxa cannot be considered as belonging to a single family.

b. *Subfamily Position*:

(1.) *Spiracles*:

Within the Lygaeidae itself the position of the abdominal spiracles has been used extensively to delimit subfamilies and it appears to conform very well to newer evidence recently brought forward from studies of the phallus, hind wings, chromosomes, nymphal morphology, inner laterotergites, etc. In the Geocorinae the spiracles are dorsal on abdominal segments 2, 3, and 4, and ventral on segments 5, 6, and 7. The only other lygaeid taxa with this arrangement are the Blediono-tinae (inclusive of the Pamphantini) and the rhyparochromine tribe Myodochini. As noted above, in *Psammium* and *Sympeplus* the abdominal spiracles on segments 2 to 7 are all dorsal and if this character is to be considered fundamental in lygaeid classification then these genera must be considered in relation to those subfamilies possessing dorsally located spiracles. These subfamilies are the Lygaeinae, Orsillinae, Ischnorhynchinae, Cyminae, Malcinae and Chauliopinae. The Blissinae and Slaterellinae possess dorsal spiracles on segments 1 through 6 with the seventh segment possessing ventrally located spiracles.

c. *Trichobothria*:

All of the lygaeid subfamilies with spiracles 2–7 dorsal (except the Psamminae) also possess one anterior and two posterior trichobothria on both abdominal segments 5 and 6. In the Psamminae only a single trichobothrium is present on segment 5 and this is placed nearly midway between the anterior and posterior margins; segment 6 possesses two trichobothria, one placed anteriorly, the other posteriorly. This combination is unique among the lygaeoid taxa. In *Slaterellus* (the only genus of the Slaterellinae) and *Heinsius* (Blissinae) the trichobothria of segment 6 are as in Psamminae, but the fifth segment also possesses two trichobothria arranged as are those on segment 6.

Both psammines lack trichobothria on segment 4, a condition also found in the Chauliopinae, Malcinae and Cyminae.

Both genera of Psamminae lack trichobothria on segment 7. In *Slaterellus* and *Heinsius*, a single trichobothrium is present on the seventh segment. In all the other subfamilies of the Lygaeidae (except the Idiostolinae which has 3) two trichobothria are present on segment 7 which is the pattern otherwise found in the Trichophora.

The variability in trichobothrial number seen in this section of the Lygaeidae is unusual as the trichobothrial number is one of the more stable characters among trichophorous Pentatomomorpha. Since the variability results from reduction, the similarities seen may be due to convergence.

d. *Abdominal scent glands*:

The dorsal abdominal scent glands of the nymphs of Lygaeidae (visible as "scars" in the adults) are generally consistent within a given subfamily or tribe. (Exceptions are known in the Ischnorhynchinae and Rhyparochrominae.) The Psamminae agree with most lygaeid subfamilies in possessing gland openings between terga 4–5 and 5–6. Of the subfamilies with spiracles 2–7 dorsal, the following possess the same scent gland arrangement: Chauliopinae, Orsillinae, Lygaeinae and some Ischnorhynchinae. The Slaterellinae and Blissinae also have the two posterior scent glands present. In the Malcinae and some Ischnorhynchinae three gland openings are present—between segments 3–4, 4–5, 5–6—which represents a more generalized condition.

The nymphs of Malcinae are unique among Lygaeidae in possessing long spines on the abdomen. The Ischnorhynchinae, although more generalized, differ in lacking inner laterotergites and having quite different genitalia.

In the Cyminae the openings are between segments 3–4 and 4–5 as noted previously for the Berytinidae and Piesmatidae. Indeed, on this basis and others, Southwood and Leston (1959) have placed the cymines in the family Berytinidae. We consider the position of the scent gland orifices a fundamental feature, and one which excludes the Psamminae from consideration as berytinids or piesmatids and obviously from the Cyminae as well.

e. *Inner laterotergites*:

The connexivum has been little used in the classification of the Hemiptera, but appears to be of considerable significance. In the Psamminae, consistent with extensive desclerotization of the terga, the inner laterotergites are reduced and apparently in the process of being lost. In *Psammium* they are present on segments 3–6, but weakly developed. In *Sympeplus* they are absent with the exception of a vestige on segment 7. This is unusual since inner laterotergite 7

is usually absent. Of the taxa with dorsal spiracles only the Orsillinae and the Lygaeinae have inner laterotergites present on segments 2–6. The Lygaeinae are unusual in having the tergum further divided by two lateral sutures. The other lygaeid subfamilies, in contrast to the Psamminae, have the inner laterotergites absent although the terga are heavily sclerotized. The Blissinae and Slaterellinae have well-developed laterotergites present on segments 3 to 6.

f. *Tarsi*:

In the Psamminae the tarsi are two-segmented—in contrast with all other Lygaeidae. The significance of the number of tarsal segments has been the subject of some controversy in hemipterological literature. It has proven to be a useful character when taken in conjunction with other characteristics, but is variable within several families such as the Reduviidae and Miridae. The two-segmented tarsi can be looked on as primitive (nymphs of Heteroptera generally possess two-segmented tarsi), a reduction phenomenon, or a neotenic condition, and must be evaluated against a character complex.

g. *Genitalia*:

The genitalia of the Psamminae are unique and have no close parallel. In the male (fig. 1) the phallotheca has no lobes and is separated from the basal apparatus by a membrane. The ejaculatory reservoir is simple and minute and the wings elongate and curved. The conjunctiva is short with no appendages present, and the vesica is short with only 2–3 turns present. There is no helicoid process present. In *Sympeplus* the vesica is distally expanded.

Of the subfamilies with dorsal spiracles, only the Malcinae and Orsillinae lack both the dorsal lobes on the phallotheca and the helicoid process, as do the Psamminae. The phallus otherwise is very different in the orsillines which possess a ring sclerite on an elongate conjunctiva and an asymmetrical vesica. The Malcinae have a large and well-developed ejaculatory reservoir with two sclerotized rods attached to it. *Slaterellus*, like the Blissinae (Ashlock 1957), also lacks processes on the phallotheca, and from the illustration (Drake and Davis 1959) probably lacks the helicoid process.

In the female the terminal abdominal segments of the psammines are as follows: the eighth tergum is composed of two widely separated sclerites; the ninth tergum is reduced to a narrow transverse sclerite with no sutures; tergum ten is relatively large and covered by the 9th valvifers. The terminal segments are rather flattened posteriorly, so that the eighth and ninth paratergites appear posterior rather than lateral to their terga, and the ninth paratergites meet behind the ninth tergum (fig. 2). The first valvifers are large, elongate, and bear short broad triangular first valvulae. The second valvifers are slender and attached by rami to the second valvulae which are

elongate and slender. In *Psammium* a small moveable appendage is present at the apex of the second valvulae. The two pairs of valvulae are *not* coadapted to each other by the usual tongue-in-groove mechanism. The spermatheca consists of a short duct with a terminal bulb. A flange runs around the proximal part of the bulb.

The cleft nature of tergum 8 is very unusual and has no parallel in the other lygaeoid groups considered here. The concealed condition of tergum 10 is also unique.

The Chauliopinae and the Malcinae have short triangular first valvulae but the second valvulae are similar, not narrow and elongated as in the Psamminae. The other subfamilies considered here have long laciniate valvulae. Moreover, the Chauliopinae differ in having an anomalous triangular sclerite present between tergum 8 and paratergite 8, and in having the ninth paratergite divided in half by a dorsoventral suture. The Malcinae have the eighth valvifers narrow and elongate and fused ventrally to each other and the ninth paratergites large and ridged to form closing valves over the genitalia.

In the lygaeid subfamilies with dorsal spiracles a spermathecal bulb with a flange is found only in the Chauliopinae. The Slaterellinae, like some Blissinae, also have a spermathecal bulb with a flange (Drake and Davis 1959).

The evidence from the genital segments is contradictory and emphasizes the isolated position of the Psamminae.

h. *Abdominal sterna*:

Sternum 7 is completely cleft in the Psamminae as is the case in all the lygaeid taxa considered, except the Malcinae and the Chauliopinae where there is no trace of a cleft. These latter subfamilies also have sterna 4 and 5 completely fused, while the psammines agree with the other lygaeid taxa in having the conjunctival membrane present between sterna 4 and 5 in the females.

i. *Additional features of the Psamminae*:

The Psamminae possess peculiar waxy scale-like hairs similar to those found in the Malcinae, Chauliopinae, Slaterellinae, and *Heinsius* (Blissinae). Similar hairs are also found in the rhyparochromine *Sisamnes*, which indicates the strong possibility of convergence.

The head lacks ocelli as is frequently the case in flightless Lygaeidae. The bucculae extend forward to meet one another and form a bulbous area, almost a "false tylus." The head is short but porrect and the juga are very short, so much so that the antenniferous tubercles extend beyond them. The head lacks all traces of long setae or spines. The bucculae are large in the Malcinae and Chauliopinae but do not extend anteriorly, and the head is extremely declivent.

The coxae are widely separated and the thoracic sterna deeply grooved to receive the labium.

j. *Conclusions*:

Within the large and heterogeneous family Lygaeidae the Psamminae occupy an isolated position and cannot be directly related to any particular subfamily and each subfamily is too specialized to give rise to the Psamminae. The Psamminae can be derived from the group of subfamilies having spiracles 2–7 dorsal, and having at least two posterior scent glands and inner laterotergites present. This group includes the subfamilies Orsillinae and Lygaeinae, each of which has some specialized characteristics. The lygaeines have a specialized subdivided terga and have connexivum 7 completely fused with tergum 7. The Orsillinae have an asymmetrical aedeagus and lack the flange on the spermatheca. This relationship probably simply reflects the more generalized condition of the Orsillinae and Lygaeinae.

The other subfamilies are highly specialized, as are the Psamminae themselves. The Malcinae and the Chauliopinae appear related to the Psamminae because of their waxy hairs, reduced ovipositor, presence of the posterior (5–6) scent gland, and in the Chauliopinae, a spermatheca with a flange. However, they could not have given rise to the Psamminae because of the fused condition of sterna 4 and 5 in the female, the uncleft condition of sternum 7, and the highly specialized genitalia present in these taxa. It should be noted that although the Malcinae and the Chauliopinae resemble each other, they are quite dissimilar in the number of scent glands, type of spermatheca, and structure of the aedeagus and abdominal terga.

Except for the crucial ventral position of spiracle 7 the Slaterellinae appear quite similar to the Psamminae. *Slaterellus* possesses inner laterotergites, the posterior scent gland, a similar spermatheca, and lacks phallothecal lobes on the helicoid process on the aedeagus.

The Slaterellinae appear to be closely related to (if not members of) the Blissinae by their closed coxal cavities, spiracle position, presence of inner laterotergites, and are distinguished by their anastomosing veins in the membrane and the presence of scale-like hairs (Drake and Davis 1959). Scudder (1962) erroneously quoted these authors as describing *Slaterellus* as having a simple aedeagus which lacks an ejaculatory reservoir. In actuality the aedeagus could not be inflated. *Heinsius* (Blissinae) has the normal blissine membrane venation, shares the scale-like hairs, spermatheca type, the peculiar loss of one trichobothrium on each segment as in *Slaterellus*, and appears to closely relate these two subfamilies.

The very different blissine habitus of *Slaterellus* suggests no very close relationship to the Psamminae, as indicated by the spiracle positions, and some similarities are probably due to convergence. This would be consistent with the zoogeographical evidence that the Slaterellinae are a specialized Australian offshoot of the Blissinae.

In view of all the features discussed above it appears that the

Psamminae is another of the small lygaeid subfamilies whose specific relationships are obscure. The phylogenetic relationships among the lygaeoid taxa are complicated by large evolutionary gaps and the occurrence of considerable convergence.

Key to the Genera of **Psamminae**

1. Antennal segments 2 and 3 subequal in length, the third segment markedly narrowed at base; metasternum with a deep median groove; claspers pointed at apex; abdominal inner laterotergites present on segments 3–6; eyes large and ovoid, not strongly reniform and not extending back over the anterolateral pronotal angles (S. Africa) ..... **Psammium**

Antennal segment 3 considerably longer than segment 2 and markedly narrowed at base to give a clavate appearance; metasternum lacking a deep median groove; claspers broad and truncate at apex; abdominal inner laterotergites absent on segments 3–6, a vestige present on segment 7; eyes more strongly reniform and extending caudad over the anterolateral pronotal angles (India) ..... **Sympeplus**

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Material Examined

Psammium mica Breddin

18 Specimens: SOUTH AFRICA: Cap. B. Sp. (De Vylder). CAPE PROVINCE: Ceres, 1–12 Nov. 1924 (R. E. Turner). In Stockholm Museum, British Museum (Nat. Hist.) and J. A. Slater collections.

Sympeplus curculiunculus Bergroth

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